SYSTEMATICS OF *PLANKTOMYA*, A BIVALVE GENUS WITH TELEPLANIC LARVAL DISPERSAL

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ABSTRACT

The small bivalve *Planktomya henseni* Simroth, 1896 (type species of *Planktomya* Simroth, 1896), originally described as a pelagic species from the North Atlantic and later recognized as a benthic Caribbean species, is redescribed and figured. New material from the Gulf of Mexico, and a possibly conspecific specimen from the Cape Verde Islands are reported. The eastern Atlantic species *Nesis prima* Locard, 1899 (type species of *Nesis* Locard, 1899), is assigned to *Planktomya* on the basis of larval shell morphology. The generic name *Planktomya* has precedence over *Nesis* (preoccupied) and over the replacement name *Monterosatus* Beu, 1971. *Planktomya prima*, which was described from the continental shelf of Bay of Biscay, occurs south to Senegal and Guinea. A new species of *Planktomya* is described from southern Angola. The systematic position of *Planktomya* is discussed on the basis of characters of the hinge, ligament and pallial line, and it is concluded that it should be placed in the Montacutidae, near *Tellimya* Brown, 1827. The current placement of *Monterosatus* in the Mesodesmatidae is rebutted. The pattern of larval dispersal, with teleplanic larvae, is briefly discussed and noted to be an extreme case of r-strategy, in which large quantities of larvae never reach an appropriate substrate on the shelf to metamorphose.

A small bivalve collected in the North Atlantic plankton and named *Planktomya henseni* by Simroth (1896) has been a quiz for malacologists since its discovery. The view that it may be the only recent example of a holopelagic bivalve was questioned by Allen and Scheltema (1972), who stated that it was immature and suggested that it probably was “the larva of a shallow-water species of Leptonacea [currently Galeommatoidea], doubtlessly one that is common and probably well-known”. Moore (1983) found a benthic species that he identified as the adult stage of *P. henseni* in sublittoral habitats of Colombia, Belize and the Bahamas, and figured it. Both Allen and Scheltema, and Moore correctly predicted that the species should be amphiatlantic, but they did not have any adult specimens from the eastern Atlantic.

From examination of material collected along the continental shelf of Europe and West Africa, it appeared that at least one other described species has *Planktomya*-type larvae. Monterosato (1875) first mentioned that species as *Nesis prima* from off Palermo, Sicily and Cap Breton, Bay of Biscay, but did not give a description. Locard (1899) made the name available and gave a description based on specimens from the continental shelf of Cap Breton. However, he did not note its peculiar prodissoconch, nor did he relate the species to the pelagic *Planktomya*. *Nesis prima* was given little attention later, and only a few more records were added from the Mediterranean (Pallary, 1900, 1920). The generic name *Nesis* is preoccupied several times, by *Nesis* Mulsant, 1850 (Coleoptera), *Nesis* Stael, 1860 (Hemiptera), and *Nesis* Conrad, 1871 (Mollusca), and the replacement name *Monterosatus* was proposed by Beu (1971). The genus was reviewed, but no new material added, by de Rooij-Schuiling (1977).

This paper is based on a reexamination of some of the available material of these species, as well as of larval shells of *Planktomya* collected on the sea floor of the northeastern Atlantic. Their relationships and taxonomic position are reassessed, and an additional species is described from southern Angola.

MATERIAL EXAMINED

MUSEUM ABBREVIATIONS.—HMNS: Houston Museum of Natural Science, Houston, Texas; MNHN: Muséum National d'Histoire Naturelle, Paris, France

Planktomya henseni Simroth, 1896

Gulf of Mexico, off Texas and Louisiana.—28°03.5′N, 94°41′W, 58 m, grab, 1 valve (HMNS 6807); 28°24.8′N, 94°41′W, 42 m, 1 valve (HMNS 6816); 28°08.2′N, 94°41′W, 69 m, 3 valves (HMNS 6817); 28°21′N, 94°35′W, 49 m, 1 broken valve (HMNS 6809); 28°22′N, 94°30′W, 16 m, 1 valve (HMNS 6803); 28°09.9′N, 94°18′W, 14 mi SSE of Galveston, 10 valves (HMNS 6812); 28°09.9′N, 94°18′W, 3–30 m, 3 valves (HMNS 6806); 28°19.7′N, 94°09.2′W, 30 m, 1 valve (HMNS 6810); 27°52.7′N, 93°50.2′W, 30 m, coral reef, 3 valves (HMNS 6804); 27°52.6′N, 93°50.2′W, 20–27 m, 9 juv. valves, 1 prodissoconch (HMNS 6819); 27°52.7′N, 93°50′W, 45–47 m, 10 juv. valves (HMNS 6814); 27°50.2′N, 93°40.9′W, 20–30 m, coral reef, 4 valves (HMNS 6805); 27°54.5′N, 93°35.7′W, 22–29 m, 2 valves (HMNS 6808); 27°54.5′N, 93°35.7′W, 22–29 m, 5 prodissoconchs (HMNS 6813); 27°53.2′N, 93°19′W, 45–51 m, 6 valves (5 juv.) (HMNS 6818); 27°57.8′N, 92°35.8′W, 54–55 m, 1 shell (HMNS 6815); 28°20.7′N, 92°26.5′W, 15–18 m, 2 valves + 2 shells (1 juv.)(HMNS 6811); total 57 valves, 3 shells, 6 prodissoconchs (valves and shells 1.4× 1.2 mm to 4.8 × 3.4 mm, prodissoconchs, including those attached to postlarval and adult valves, 0.90 to 0.95 mm).

Planktomya cf. *henseni*

Cape Verde Is., Fogo.—RV CALYPSO sta 34 1 live-collected spec. (4.3 × 3.2 mm, prodissoconch 0.93 mm)(MNHN).

Planktomya prima (Locard, 1899)

Bay of Biscay, 'Capbreton 88' expedition (MNHN).— 43°40.0′N, 01°48.1′W, 134 m (sta DE 01), 3 valves; 43°57.4′N, 02°05.2′W, 164 m (sta DE 05), 5 valves; 43°22.8′N, 01°59.2′W, 94 m (sta DR 11), 3 valves; 43°33.7′N, 01°49.8′W, 188 m (sta DR 18), 3 valves; total 14 valves (3.4 × 2.2 mm to 6.7 × 4.3 mm, prodissoconchs attached to adult valves, 1.0 to 1.1 mm).

Algeria.—Oran, 2 valves in Locard collection, (7.5 × 4.3 mm; 6.3 × 3.9 mm)(MNHN).

Morocco.—Off Melilla, 50 m, the spec. figured by Pallary (1920: 92, pl. 1 figs. 47–49)(5.1 × 3.3 to 5.3 × 3.3 mm)(MNHN).

Portugal.—37°01.2′N, 09°02.8 W (RV FAIAL sta P28), silty mud, 100 m, 1 valve (6.4 × 4.0 mm; prodissoconch 1.0 mm)(MNHN); Mission Algarve 1988, off Burgau, 37°03.4N, 09°46.3′W, 35 m, 1 v. (7.8 × 5.2 mm, prodissoconch 1.0 mm)(MNHN).

Senegal.—Off Dakar, 14°51.5′N, 17°30′W, 165-180 m, 2 valves, leg. Marche-Marchad (5.4 × 3.4 to 6.8 × 4.2 mm); South of Gorée, 95–98 m, 4 valves, leg. Marche-Marchad (5.3 × 3.1 to 6.1 × 3.5 mm); South of Gorée, 39 m, leg. Marche-Marchad (8.8 × 5.1 to 9.2 × 6.0 mm) (MNHN).

Guinea.—9°30′N, 16°00′W, 113 m (Sedigui 1 sta 221), 1 valve, leg. Cosel 1988 (6.8 × 4.4 mm, prodissoconch 1.15 mm) (MNHN).

Planktomya magna n. sp.

Angola.—The type material and: Bay of Lucira (Doca), 10–20 m, 1 valve; Praia Amelia, 40–60 m, 1 valve.

Planktomya sp. (larval shells from the sea bottom)

Cape Verde Basin, 'Eumeli 2' box cores.—18°31'N, 21°W, 3107 m (KG 12), 1 shell; 18°34'N, 21°02'W, 3139 m (KG 13), 2 shells; 18°35'N, 21°00'W, 3137 m (KG 30), 3 shells; 20°29'N, 18°30'W,

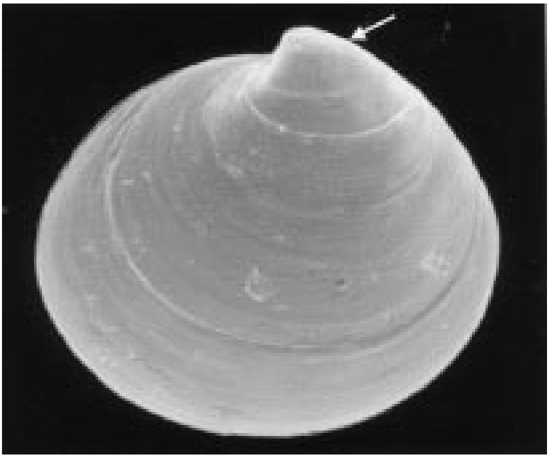

Figure 1. Larval shell of *Planktomya* sp. from the sea bottom in Cape Verde Basin, (18°35′N, 21°00′W, 3137 m; MNHN), external view (actual size 1.2 mm). Arrow indicates the limit of prodissoconch 1.

1618 m (KG 39), 6 shells; 20°32’N, 18°30’W, 1590 m (KG 40), 3 shells; 20°35’N, 18°30’W, 1598 m (KG 41), 4 shells; 20°35’N, 18°32’W, 1820 m (KG 42), 3 shells; 20°32’N, 18°35’W, 1970 m (KG 44), 2 shells; 20°29’N, 18°35’W, 1999 m (KG 45), 1 shell; 20°29’N, 18°32’W, 1789 m (KG 46),7 shells; total 32 shells.

Tellimya ferruginosa (Montagu, 1803)

France, Channel coast—Wimereux, 4 spec., leg. Giard (4.7 × 2.7 to 8.8 × 4.7 mm)(MNHN).

France, Bay of Biscay, ‘Capbreton 88’ expedition (MNHN).—43°40.0′N, 01°48.1′W, 134 m (sta DE 01), 8 valves; 43°57.4′N, 02°05.2′W, 164 m (sta DE 05), 1 spec.; 43°22.8′N, 01°59.2′W, 94 m (sta DR 11), 20 valves; 43°33.7′N, 01°49.8′W, 188 m (sta DR 18), 5 valves.

GENERAL FEATURES OF *PLANKTOMYA*.—All the species considered herein share a peculiar morphology of the larval shell, and also some characteristics of the adult which will be summarized here and will not be repeated in the species descriptions.

GENERIC DESCRIPTION.—Larval shell (Fig. 1) reaching 0.9 × 0.7 mm to 1.2 × 1.0 mm at metamorphosis, brownish in color and made of a flexible, translucent organic material. Beaks posterior to midline, at 2/3 of larval shell length. Prodissoconch 1 cap-like, inconspicuous, approximately 0.18 mm in diameter; prodissoconch 2 with outer surface covered by rather fine commarginal growth lines. Inside with a strong buttress which starts at some distance behind the beaks and extends downwards.

Adult shell ovate-elongate in outline, up to 11.7 mm long and 7.8 mm high, with slightly convex valves. Beaks situated at posterior 2/3 to 3/5 of shell length. Prodissoconch eroded and seen as an internal mold, with a distinct groove (mold of former internal buttress) posterior to the beaks. Outer surface of dissoconch with commarginal growth lines or threads.

Hinge line on left valve with one large cardinal tooth pointing toward the anterior part of the ventral margin, and posterior to it a broad resilifer, open through the entire hinge plate beneath the umbo. Hinge line on right valve also with one large cardinal tooth, anterior to it a socket for the tooth of the left valve, and posterior to it the resilifer which also reaches through the hinge plate to the umbo. A small projecting flap, more or less

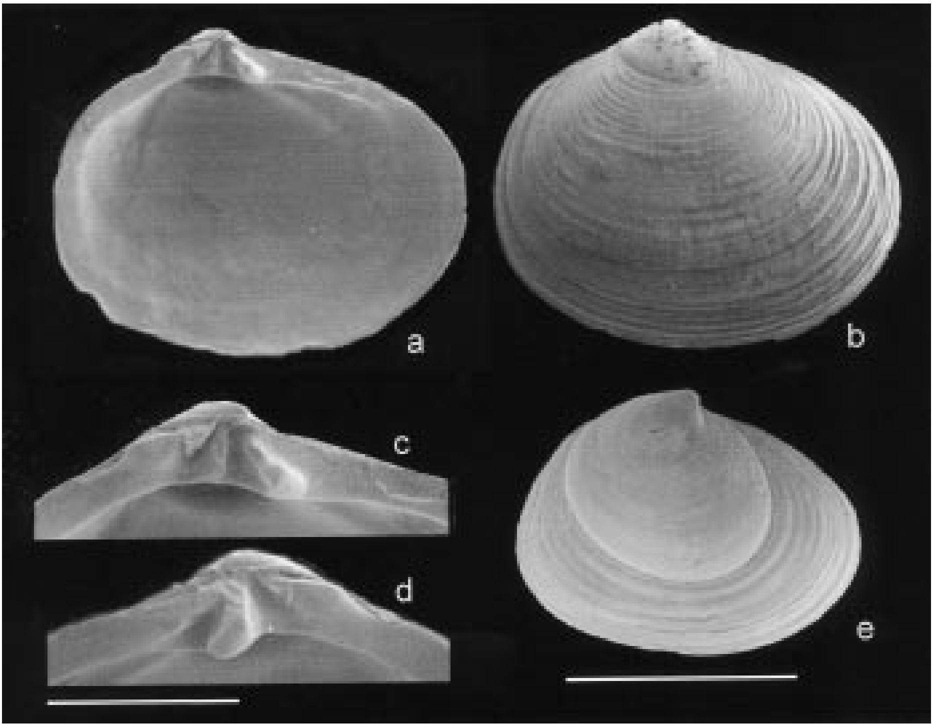

Figure 2. *Planktomya henseni* Simroth, 1896, from off Louisiana. a. adult shell (27°57.8′N, 92°35.8′W, 54–55 m; HMNS 6815), interior of left valve (actual length 3.7 mm). b. exterior of right valve of the same specimen. c. detail of hinge of the left valve. d: detail of hinge of the right valve; e. juvenile specimen (28°20.7′N, 92°26.5′W, 15-18 m; HMNS 6811). Scale bars 1 mm.

apparent, on postero-dorsal margin just behind the umbo on each valve. Pallial line entire, thick, with a ragged inner edge. Adductor muscle scars equal in size, the anterior tapering toward the umbo, the posterior rounded.

Planktomya henseni Simroth, 1896
(Fig. 2)

Planktomya henseni Simroth, 1896: 28–31, pl. 1 fig. 1a–c.

Type Material.—The figured spec. of Simroth (1896: fig. 1b) is here designated as lectotype.

Type Locality.—Hereby restricted to Plankton-Expedition sta 37, Sargasso Sea (32°N, 59°W), surface waters.

Redescription Based on Adult Shells.—Shell up to 4.8 mm long and 3.4 mm high, ovate in outline, inequilateral, with slightly convex valves. Beaks situated at posterior 3/5 of shell length. Anterior part of dorsal margin gently curved, gradually merging into the evenly rounded anterior margin. Ventral margin also gradually meeting the anterior margin, regularly rounded and gradually merging into the rounded posterior margin and thence to the sloping postero-dorsal margin. A very small projecting flap, usually not visible from the outer side, on postero-dorsal margin just behind the umbo.

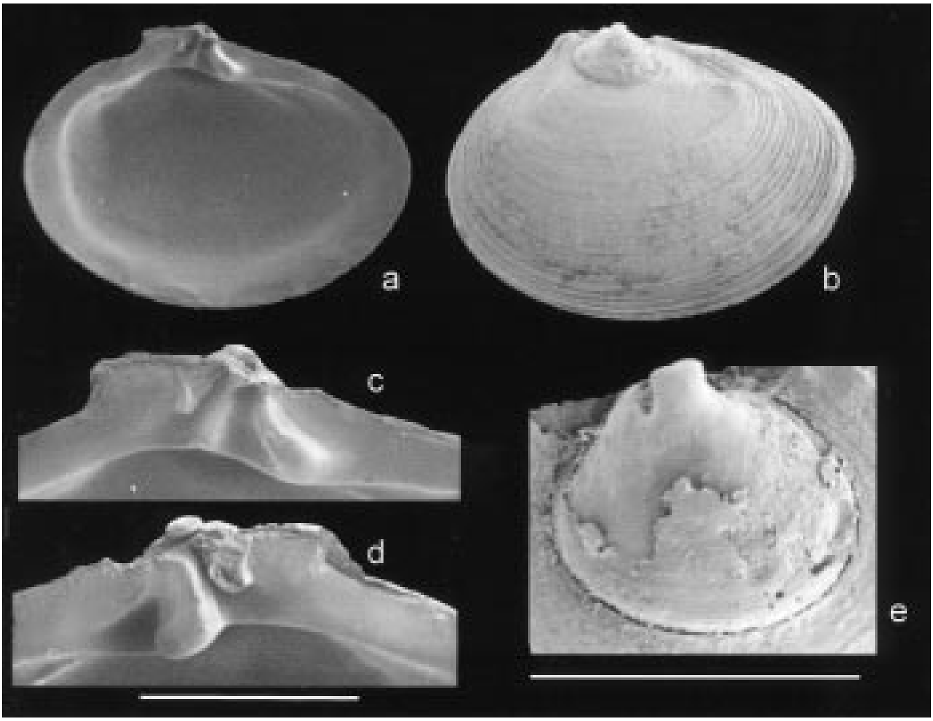

Figure 3. *Planktomya* cf. *henseni* Simroth, 1896, shell of adult specimen from Fogo, Cape Verde Islands (MNHN). a. interior of left valve (actual length 4.3 mm). b. exterior of right valve of the same specimen. c. detail of hinge of the left valve. d. detail of hinge of the right valve; e. detail of the prodissoconch, the apical part preserved as internal mold. Scale bars 1 mm.

Hinge line very thick, with a broad resilifer, open through the entire hinge plate beneath the umbo; teeth as in generic description. Pallial line entire, thick, with a very ragged inner edge.

Exterior of valves with internal mold of prodissoconch 0.90 to 0.95 mm long, 0.7 mm high. Outer surface with a sculpture of distinct, fine commarginal threads.

Remarks.—This species was originally described from specimens in the larval stage, and that description alone does not allow it to be identifed unambiguously to one of the species treated here. The most species-specific character at the larval stage is the size, and Simroth (1896) did not give any precise size indication. If considering the indications he gives for magnification, the specimen should be approximately 0.55 mm long which anyway does not correspond to a full grown larva. In order to support Moore’s (1983) interpretation of this being the dominant Caribbean representative of the genus, I propose to restrict (by this lectotype designation) the type locality to the Plankton-Expedition locality nearest to the Caribbean Sea.

One specimen from the Cape Verde Islands (Fig. 3), tentatively assigned to this species, was collected alive and contained dried soft parts. Examination of the rehydrated specimen suggests that only one demibranch is developed. The little projecting flap posterior to the umbos is more expressed in this West African specimen than in the Caribbean material, and the outline is also slightly different, with a more produced anterior margin. However, the flap can be discerned in the Gulf of Mexico specimens and this variation

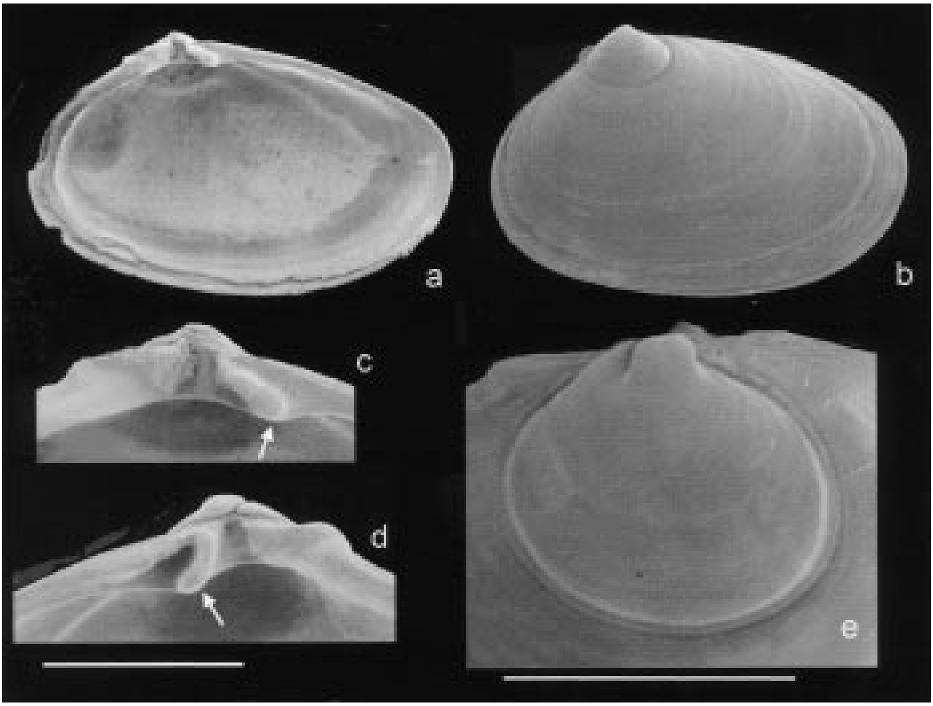

Figure 4. *Planktomya prima* (Locard, 1899), adult shells from Cap Breton, Bay of Biscay (MNHN). a. interior of a left valve (actual length 5.2 mm). b. exterior of a right valve of another specimen (actual length 5.0 mm). c. detail of hinge of the left valve. d. detail of hinge of the right valve; e. detail of the internal mold of the prodissoconch. Scale bars 1 mm, arrows point to cardinal teeth.

does not warrant a distinction at the species level. The strong external sculpture makes a clearcut difference with the predominantly eastern Atlantic *P. prima* and *P. magna*.

Planktomya prima (Locard, 1899)
(Fig. 4)

Nesis prima Locard, 1899: 135–136.

Types.— Could not be located in Locard collection (MNHN), and were already missing at the time of Lamy (1914).

Type Locality.—Cap Breton canyon, Bay of Biscay, France.

Redescription.—Shell up to 9.2 mm long and 6 mm high (usually somewhat less), elongate-ovate in outline, inequilateral, with quite convex valves. Beaks situated at posterior 2/3 of shell length. Anterior part of dorsal margin gently curved, gradually merging into the evenly rounded anterior margin. Ventral margin also gradually meeting the anterior margin, gently and gradually merging into the rounded posterior margin and thence to the sloping postero-dorsal margin. A small but conspicuous projecting flap, also visible from the outer side, on postero-dorsal margin just behind the umbo.

Hinge line and teeth as in generic description. Pallial line entire, thick.

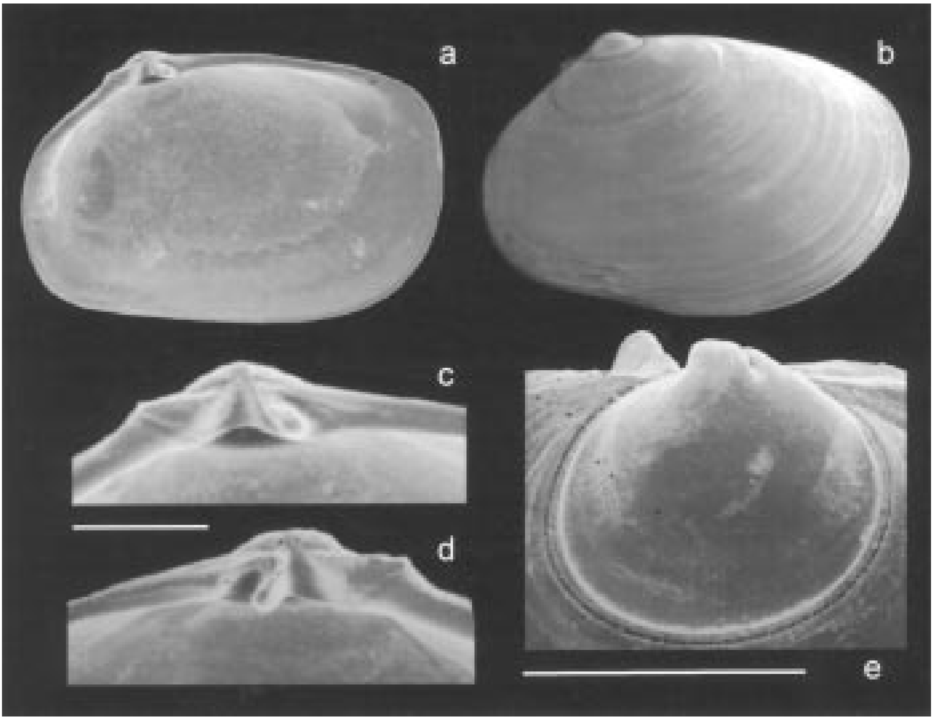

Figure 5. *Planktomya magna* n.sp. (all MNHN). a. interior of the holotype from Bay of Lucira, Angola (left valve, actual length 9.3 mm). b. exterior of a paratype, same locality (right valve, actual length 9.1 mm); c. detail of hinge of left valve. d. detail of hinge of right valve; e. detail of the internal mold of the prodissoconch of another paratype. Scale bars 1 mm.

Exterior of valves with internal mold of prodissoconch 1.0 to 1.15 mm long, 0.9 to 1 mm high. Outer surface quite smooth, with only growth lines and some marked growth stages.

Remarks.—This species was accurately redescribed and reviewed by de Rooij-Schuiling (1977); her excellent figure of Locard's specimens from Algeria shows clearly the *Planktomya* prodissoconch, but no relation was made with *Planktomya*. Monterosato's specimen from Palermo (now in Museo di Zoologia, Rome) was figured by Gaglini (1994) and her photographs also show the prodissoconch. The species is here for the first time assigned to the genus *Planktomya*.

Planktomya magna new species
(Fig. 5)

Type Material.—Holotype (Fig. 5A, left valve, 9.3 × 5.8 mm) and paratype (Fig. 5B, right valve, 9.1 × 5.8 mm) from the type locality, leg. Gofas 1985, MNHN. Paratypes (5 left valves and 4 right valves) from Angola, Bay of Lucira (Bissonga: 13°51′S, 12°31.5′E, 10–20 m in coralline algae), leg. Gofas 1985, MNHN.

Type Locality.—Angola, Bay of Lucira (Praia do Cesar: 13°52.5'S, 12°30.0'E, 10–20 m in coralline algae).

Description.—Shell up to 11.7 mm long and 7.8 mm high, elongate ovate in outline, inequilateral, with slightly convex valves. Beaks posterior to midline, situated at about 2/3 of shell length. Anterior part of dorsal margin gently curved on most of its extension, then abruptly curved to meet the anterior margin. Ventral margin gradually meeting the anterior margin, swollen in its anterior section, then rather straight until it meets the posterior margin at an abrupt curve. Posterior margin somewhat truncated, then meeting the sloping postero-dorsal margin. A small projecting flap on postero-dorsal margin just behind the umbo.

Hinge line and adductor muscle scars as in generic description. Pallial line clearly visible, entire, with a very ragged inner edge.

Exterior of valves with scar of prodissoconch 1.2 mm long, 1 mm high. Outer surface smooth, with only growth lines apparent.

Remarks.—This species resembles *P. prima* in having a smooth external surface of the teleoconch. It differs is reaching a slightly larger size, having a flatter anterior portion of the valves and a different outline with produced anterior part of the ventral margin, and more angular posterior profile.

DISCUSSION

PLANKTOMYA AS A VALID GENERIC NAME.—The larval shells of the three species treated herein are very similar, and cannot per se be reliably identified to species level. Nevertheless, the Caribbean material described by Moore (1983) and herein seems to belong to a single species. For this reason, I agree with Moore in using the specific name *P. henseni* for this Caribbean species. The alternative course would be to use the generic name *Planktomya* only in a descriptive, vernacular sense (in the same way as ‘sinusigera’ or ‘echinospira’ is used for some gastropod larvae) and to describe the Caribbean species as a new species of *Monterosatus*. However, this does not comply with the rules of zoological nomenclature, which treat as available a name based on part of an animal (here, the larval shell). The suppression of *Planktomya* would thus need a ruling of the Commission which I am not convinced to be justified.

THE SYSTEMATIC POSITION OF *PLANKTOMYA*.—*Planktomya* was not assigned to a family in the original publication, and the larval shell does not resemble any other known bivalve prodissoconch. *Planktomya* was listed as *incertae sedis*, and *Nesis* was omitted in the Treatise on Invertebrate Palaeontology (Moore, 1969). Allen and Scheltema (1972) tentatively assigned *Planktomya* to the Leptonacea [currently Galeommatoidea], following an indication by Kurt Ockelmann that the interlocking structure of the ventral shell margins could be observed in postlarvae of various species in that superfamily. Moore (1983) agreed with this and placed *Planktomya* in the Sportellidae, which he considered to belong within the Leptonacea. However, the position of the Sportellidae is unsettled, and the general trend is to place them in the Cyamioidea (Thiele, 1934; Coan, 1999), among which both siphons and a pallial sinus are present.

Nesis, or *Monterosatus*, had a quite different treatment. Locard (1899) placed it in the Mactridae, and later Sacco (1901) included it, with doubt, in the Mesodesmatidae. This was formalized by Nordsieck (1969) and Beu (1971), who placed *Nesis* or *Monterosatus* in the Mesodesmatidae, thus interpreting the ligament as being borne on an internal chondrophore. This placement was endorsed by de Rooij-Schuiling (1977) in a review of the genus.

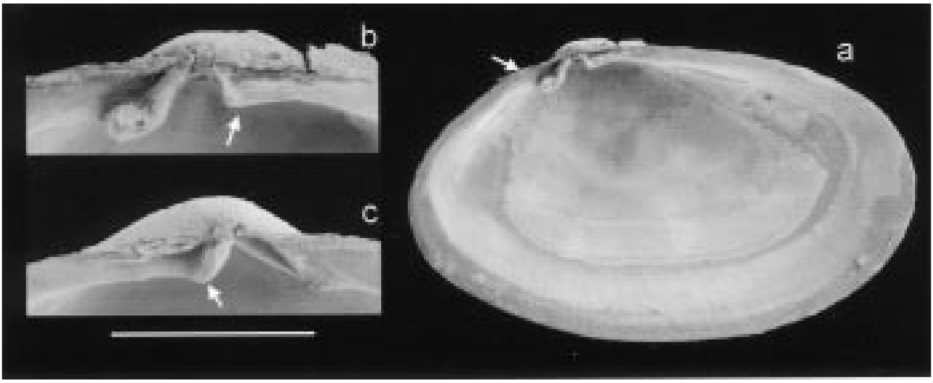

Figure 6. *Tellimya ferruginosa* (Montagu, 1808), shell of a specimen from Wimereux, France (MNHN). a. interior of the left valve (actual length 6.4 mm; arrow points to the flap posterior to the umbo). b. detail of hinge of the left valve. c. detail of hinge of the right valve. Scale bars 1 mm, arrows point to cardinal teeth.

The evidence from the shell characters suggests that this is not correct. The Mesodesmatidae have a distinct pallial sinus posteriorly, whereas the pallial line of adult *Planktomya* is entire and indicates that there are no siphons. The hinge of Mesodesmatidae is also very different, with a triangular cardinal on the right valve fitting between two cardinals of the left valve, and with well developed anterior laterals.

On the other hand, the hinge architecture of *Tellimya* (Montacutidae) is so similar to that of *Planktomya*, that all the structures can be recognized (Fig. 6). The internal ligament of *Tellimya* is very strong and has an important role in the articulation of the valve, whereas the teeth appear less developed. *Planktomya* also shares with *Tellimya* the presence of a projecting flap posterior to the umbo, the similar ragged aspect of the inner edge of the pallial line, and similar outlines of the adductor scars. Nothing is known of the soft parts of adult *Planktomya*, except that the observation of a dried body inside a specimen from the Cape Verde Islands suggests that only one demibranch is developed, as in *Tellimya* (Pelseneer, 1911). From what can be seen of shell morphology, I suggest that *Planktomya* be placed with *Tellimya* in the Montacutidae. The main difference, which justifies keeping *Planktomya* and *Tellimya* as separate genera, lies in the fact that the left valve has a distinct, functional tooth, which is not expressed in *Tellimya*.

PATTERN OF LARVAL DISPERSAL.—*Planktomya* species are rare as adults. The material of *Planktomya prima* (14 valves) listed from the CAPBRETON cruise in the Bay of Biscay comes from a sampling effort of eight completely sorted dredge hauls in an appropriate habitat, which yielded 70 species of bivalves represented by over 2000 specimens or shells; yet this is the largest single catch of *P. prima* known in European collections. Moore (1983) correctly stated that this is an elusive animal, where the seven valves and one juvenile complete shell were the only material he could obtain in 20 yrs of extensive collecting in the Caribbean. A similar conclusion can be drawn from the material in the Houston Museum of Natural Science, where the 60 shells or valves mentioned here are the only material of *Planktomya* in approximately 20,000 lots collected in a general survey of Gulf of Mexico.

Conversely, larval *Planktomya* are common in Atlantic plankton tows and their shells are abundant on the bottom of the deep sea. Allen and Scheltema (1972) found over 3000 specimens in 594 out of 900 plankton tows in the northern Atlantic. In the EUMELI cruises off Northwestern Africa, 32 shells of *Planktomya* were found in 10 out of the 40 box cores studied. With each core sampling a surface of 0.25 m^2 (Cosson, 1996), this suggests a density of 3 shells m^{-2} on the sea bottom, a figure consistent with the densities of 0.1 to 0.5 specimen m^{-3} stated by Allen and Scheltema (1982) in comparable areas.

However tentative these figures may be, they indicate that the larvae are exceedingly common compared with the adults, and that probably a very small number of them reach an appropriate substratum to grow into reproducing adults. The pattern of larval dispersal in *Planktomya* species implies an enormous waste of larvae which drift over the deep sea, and can be seen an as extreme case of r-strategy (MacArthur, 1972). This can continue as long as enough larvae reach suitable environments to ensure the continuity of populations, and does not affect very much the allocation of resources by the benthic population, because the bulk of the investment is made by the planktonic community in which the larvae live and feed.

Given the potential for dispersal found in *Planktomya*, it might seem unlikely that more than one species be present in the Atlantic Ocean. However, the morphological differences are such so as not to leave any doubt regarding the validity of the species. A climatic gradient can be seen between the ranges of *P. henseni*, essentially intertropical, and the other two species found in temperate areas of the Northern and Southern Hemispheres respectively. There are other examples of such species pairs or series with planktotrophic larvae (see Gofas, 1999, for examples in the gastropod family Rissoidae) or even among holoplanktonic species.

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